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Botanical evidence for quaternary climates in Africa

INTRODUCTION

The distribution of living organisms is, to a great extent, determined by the trends of evolution and by former and present climates. Plants in particular are very sensitive to climate and with sufficient knowledge of plant ecology we can use a vegetation map to obtain valuable information on the complex of factors which is known as "climate". Climatologists therefore make much use of vegetation maps and compare their climatic regions with the vegetation pattern. Land animals depend, directly or indirectly, so much on plant life that their distribution often coincides closely with that of plant communities.

Before considering the relation between climate and plant distribution in former times, we will pay attention to the present-day problem. In analysing the relation between climate and the vegetation pattern we have mainly to consider humidity and temperature. These are determined by many causes such as solar radiation, latitude, cloudiness and a great variety of other factors which depend on the characteristics of the locality. The fact that temperature and humidity are to a great extent interdependent makes it impossible to separate their respective influences in plant ecology. This difficulty has also been encountered by climatologists who try to express the climatic factors in formulae with which they make their maps of the climatic regions, closely resembling the vegetation maps. These classifications accept the plant as a "meteorological instrument" which is capable of measuring all the integrated climatic elements (Trewartha 1954). The climatic classifications of both Köppen and Thornthwaite are not entirely successful from the botanist's point of view (Schulze 1947). I wish to mention a few examples to illustrate this. The big region of the dry hot steppe climate of Köppen (B. Sh. w.) and Thornthwaite (D. B'd.) is not a natural unit as it covers the Kalahari thornveld, the Mopane area, the sweet grassland and also the false Upper Karoo (Acocks 1953). This region should certainly be subdivided (Schulze, *loc. cit.*). Other discrepancies in the classification of Köppen are found in the wide woodland belt which crosses Africa south of the equator and in both systems there are inconsistencies in the area of southern Ethiopia and northern Kenya.

The climatic regions described for South Africa by Jackson (1951) generally give a better approximation of the botanical areas than the above-mentioned systems. The maps of Köppen and Thornthwaite certainly do not correspond well with the vegetation map published in 1959 for Africa south of the Tropic of Cancer (Keay 1959). But our vegetation maps also

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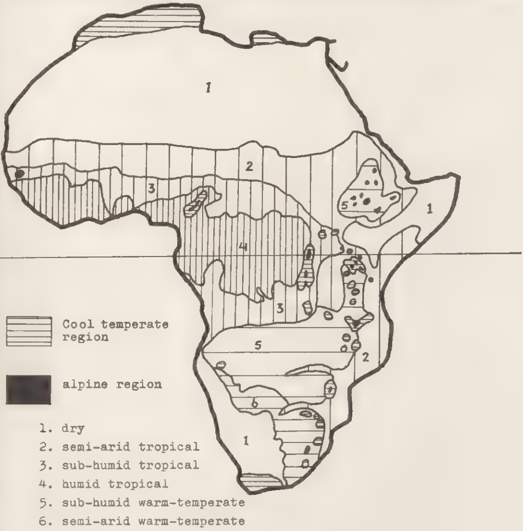
have their shortcomings. One of these on the last-mentioned map is the fact that the tropical lowland climate of the Moçambique plain is not clearly shown on it because the woodland belt, which also covers this area, is not sufficiently subdivided.

Climatic changes inferred from the present day Vegetation Pattern

The problem of describing present-day climate using the evidence provided by the vegetation pattern has not yet been solved as the vegetation shows a great variability and a refined



MAP I · THE PRINCIPAL CLIMATIC-ECOLOGICAL REGIONS OF AFRICA.

sensitivity for the complex factors of climate. A detailed study of plant distribution however reveals a considerable number of "irregularities", which give convincing indications for the understanding of the dynamic nature of climate. Our discussion will try to throw more light on those changes in climate which have especially occurred during the Quaternary. This evidence is strongly connected with plant migration, a subject which has been treated in a separate contribution to this symposium.

For our considerations it is important to recognise only the main climatic regions with special reference to plant ecology. Without going into details, such as the seasonal distribution of rainfall, these regions can be characterised as follows (Map I):

	Precipitation in mm. per annum	*Mean July temperature in °C*
Dry	<250	—
Semi-arid tropical	250—1,250	≧18
Sub-humid tropical	1,250—1,500	≧18
Humid tropical	>1,500	>20
Sub-humid warm-temperate ..	500—1,250	<18
Semi-arid warm-temperate ..	250—500	<18

Two other climatic–ecological regions are more difficult to define in terms of temperature and rainfall. They are: The *cool temperate region* which includes the winter rainfall areas and the habitat of the temperate and montane forests; and the *alpine region* on the mountains above the tree-line.

Some of the important floras of which elements occur in Africa are the following (Map II):

The Palaeotropical Flora of Africa, which inhabits the tropical, the warm-temperate and the desert regions. Many elements of this flora will most probably belong to the autochthonous flora of Africa and can therefore, in accordance with the proposal made by Burbidge (1960) for Australia, be named the *priscotropical African Flora*.

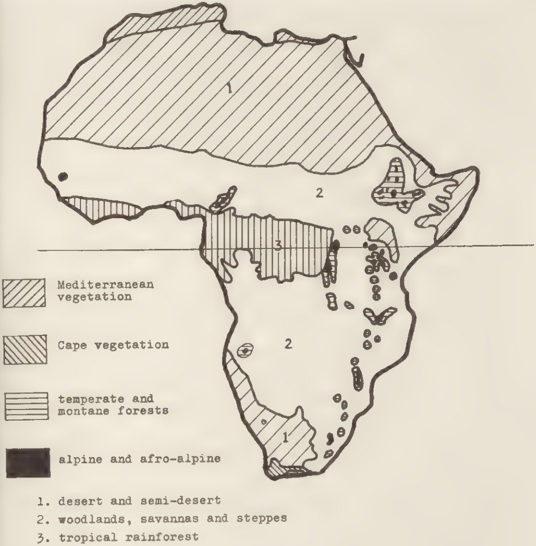
The Mediterranean Flora, which occurs in the cool-temperate region along the northern coast of Africa. This flora is not related to the proper African flora, but to the arcto-tertiary flora of the Northern hemisphere.

The Cape Flora, which is a rich sclerophyllous flora and the southern counterpart of the Mediterranean flora. Two elements of this old flora, the Proteaceae and the tribe Ericeae of the Ericaceae family, are important for our climatic considerations and will be discussed.

The Montane and Temperate Forests occur in isolated patches from the coast of the Cape along the eastern escarpment northward, where they merge into the montane forests. It is not customary to consider these forests as one entity, but we wish to treat them together, because they show taxonomic affinities and because they prefer a climate which is moister than that of the Cape Flora (Aubreville 1949). These forests show affinities with the Holarctic region, with the African humid tropical region and probably also with Antarctica.

The Alpine Holarctic Flora, of which elements are mainly found on the mountains along the eastern side of the continent as far south as Basutoland; and few of them spread further south into the cool temperate region. These Holarctic genera live isolated in the greater part of Africa as there does not exist a continuous high mountain range as in America. They must be of Tertiary age.

The Semi-desert Karoo Flora is supposed to be of a mixed origin. The affinities of this flora, which is rich in undershrubs, point more to the Cape Flora than to the tropical African Flora (Acocks 1953).


1
2
3
2
1
Mediterranean vegetation
Cape vegetation
temperate and montane forests
alpine and afro-alpine
1. desert and semi-desert
2. woodlands, savannas and steppes
3. tropical rainforest

MAP II SOME IMPORTANT VEGETATION TYPES OF AFRICA.

These floras form at present the pattern of the African vegetation. During Quaternary times these floras changed their areas very often, they advanced and retreated, and consequently possess many relic and pioneer stations outside their proper continuous areas. The climatic inference which can be made from the occurrence of these disjunct little areas will be discussed now.

With regard to the *Palaeotropic Flora of Africa*, the tropical rain forest gives the best example for our discussion. A great number of isolated rain forest clumps occur in the sub-humid tropical region in Angola, Northern Rhodesia, Tanganyika, Uganda, etc. These patches show clear affinities to the tropical rain forest and mostly occur at sheltered positions, along drainage systems and near swamps. They are even sometimes found at higher altitudes outside the tropical region in the sub-humid warm-temperate area. Their composition and ecology is entirely different from that of the surrounding dry tropical woodland (Trapnell 1953).

These rain forest clumps are relics of former wetter conditions during the Quaternary and are rapidly disappearing through human influence. Their history can probably be studied with the help of pollen analysis coupled with radio-carbon dating.

The Mediterranean Flora is sharply separated from the flora of Central Africa by the Sahara desert and only very few elements have passed this barrier and entered the equatorial region of Africa. Remnants of this flora however still occur in very isolated localities in the desert. During late Quaternary times, until only a few thousand years ago, the desert was however covered over vast areas with a sclerophyllous Mediterranean vegetation. The small refuges, which still exist, indicate a recent desiccation.

A number of genera of the *Cape Flora* are found widely scattered along the eastern escarpment and on the mountains and plateaux of East Africa but some also occur isolated in S.W. Africa (Rennie 1935), in Angola and West Africa. The origin of this flora has been much discussed in recent times (Beard 1959, Good 1953, Levyns 1952, Adamson 1958 and 1959).

Two elements of this flora will be considered in some detail: the Proteaceae and the tribe Ericeae.

The Proteaceae can be divided into two subfamilies. The subfamily Persoonioideae which occurs in the temperate regions of Australia and Africa differs from the more tropical subfamily of the Grevilleoideae. This last mentioned subfamily is found in South America, N.E. Australia and other eastern territories.

There is much controversy about the origin of this family (Levyns 1958, Vogts 1960, Beard 1959). The idea of a northern origin of the Proteaceae has been put forward on several occasions, but the evidence supporting this theory is not convincing as far as fossil leaves, fruits and pollen grains are concerned (Burbidge 1960, Kräusel 1958, Good 1953). Recent finds of fossil pollen in Russia have not yet been published (personal communications by Mrs. M. M. Vogts and Mrs. S. Samoilovitch).

The distribution pattern of this family strongly indicates a southern origin from the Antarctic continent. The subfamily Persoonioideae is of Afro-Australian affinity. The description of its dissemination in Africa by Beard (1959) gives a clear picture of the origin of its present area in Africa. The less highly developed types have a continuous distribution in the vast woodlands of Southern and East Africa and in the East African montane vegetation belt. They only avoid the deserts, semi-deserts, the humid tropical region and the temperate grasslands. This fact gives us little opportunity for climatic indications of fossil and recent material, as they inhabit a wide range between 1,200 and 3,800 m. altitude. The final migration of the African Proteaceae to the S.W. Cape, where they developed a secondary centre, has been made very acceptable by Beard (1960) and Levyns (1958).

Other elements of the Cape Flora, such as the tribe Ericeae, are much more important for climatic inference. The origin of this tribe could have been in tropical Africa (Good 1953). This point will only be better understood after the distribution and cytotaxonomy of the ca. 16 Central African species will have been studied.

More than 600 species of this tribe occur at the S.W. Cape. Here they grow down to sea-level, but further north the related species grow at much higher altitude. In the Drakensberg they occur above 1,000 m., in Rhodesia their minimum altitude is 1,300 m., and in Southern Tanganyika they are a typical feature of the vegetation wherever the country reaches an altitude of at least 2,000 m. In East Africa the montane forest favours the same altitude as the Ericaceae and these are therefore found in two belts: scattered below the forest at about 2,000 m. and in bigger concentrations above the forest at altitudes between 3,300 and 4,700 m.

The Ericaceae are thus plants with a narrower ecological amplitude than the Proteaceae and are consequently of greater importance as climatic indicators. They are chiefly confinde to the cool-temperate and alpine habitats and occur only scattered in the sub-humid warm-temperate region. Their isolated occurrence, as for instance in many relic stations in Tanganyika, clearly point to former wetter and cooler conditions during the Quaternary.

Many relics of the *Montane and Temperate Forests* still occur from the Knysna forest at the southern coast of the Cape Province northward along the eastern escarpment. These forests are for instance found in the Drakensberg, Inyanga, the Pungwe Mountains and on the isolated volcanoes along the rift valleys. In East Africa the montane forest is sandwiched in the Ericaceous area and usually dominates on that part of the mountain slope which has a cool-temperate climate and which receives the maximum rainfall. The small forest clumps which still occur on some mountain ranges in Northern Rhodesia, as for instance near Mpika at 1,900 to 2,000 m., and in Southern Tanganyika at 2,100 m., are striking examples of a dwindling vegetation type, which is entirely different from the surrounding dry woodland. The same trend of desiccation during the post-Pleistocene is indicated by the clumps of *Arundinaria* which are found scattered in the woodland of southern Tanganyika at about 2,000 m., altitude.

Moreau (1933) has studied the possible former greater area of these forests during more humid periods in East Africa in connection with zoogeography.

Regarding the *Alpine Holarctic Flora*, in the afro-alpine flora of East Africa a number of genera which are of boreal affinity, occur such as: *Delphinium*, *Dipsacus*, *Burtsia*, *Anthriscus*, *Valeriana*, *Epilobium*, *Carduus*, *Crepis*, *etc*. (Engler 1892, Hedberg 1957). In the alpine region of Basutoland we find species of *Myosotis*, *Ajuga*, *Bromus*, *Hypericum* and *Cerastium*, which are also of northern origin.

The number of northern elements in the vegetation of the high African mountains, especially in East Africa, is much bigger than the number of Cape plants. This could indicate that the Cape Flora was not able to adapt itself so well to the alpine conditions.

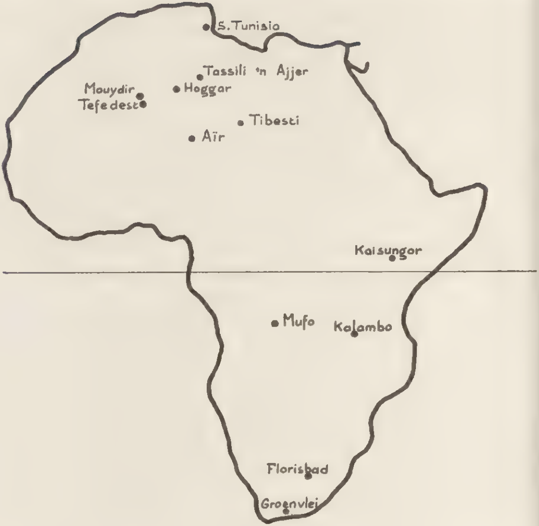
According to the speciation which took place, these alpine elements must be very old. Because of their strict isolation, they possess no advance or relic stations but pollen analysis may be able to use these elements as climatic indicators.

The many patches of *Semi-desert Karoo Flora*, which occur north of its present area as far as the northern Orange Free State, have often been used as an indication of desiccation. It has been made very plausible that human influences played a strong part in this rapid northward advance of the Karoo in historic time. During the many arid periods which occurred in the Tertiary, the Karoo Flora must have been widespread in Southern Africa (Acocks 1953).

The above-mentioned evidence indicates that the more humid vegetation types have been retreating during the latter part of the Quaternary. The Cape and Mediterranean Floras, the tropical rain forest and the montane and temperate forests, all left relicts in their wane. Warmer and drier climatic oscillations must have been responsible for this general reaction of the vegetation.

STUDY OF FOSSIL POLLEN (MAP III).

The study of plant geography can supply us with strong evidence for former climatic changes as we have seen in the discussion about relic vegetation, but the time and the extent of these changes is very difficult to assess. Study of fossil pollen should give more accurate information on the time and nature of the climatic oscillations, if only more pollen-bearing



MAP III. LOCALITIES OF FOSSIL POLLEN SITES.

deposits were available. Climate in Africa is, in general, not favourable for the preservation of fossil pollen and shorter or longer periods of dryness have destroyed much valuable material. Pollen is, however, well preserved in wet deposits round permanent springs and in moist mountain regions. The difficulties in explaining former climates with the aid of palaeobotany are more complicated than the analogous recent problems, because in this case it is not only the climate which is unknown, but also our knowledge of the site itself raises specific problems. The site may have been a niche with a vegetation which was not representative of the former general climate; or the assemblage of fossils may represent only a stage in the succession of the vegetation and not the climax vegetation. So far a limited number of analyses have been made and it should be borne in mind that these first results have only a limited application as they are too far apart to allow valid detailed conclusions. I will discuss the palynological evidence as far as it is available for Africa.

The high mountains provide a very important starting point in East Africa, where pollen-bearing deposits occur and where the pollen diagrams can be coupled with the glaciology of the mountains. Several palynologists are at present engaged in this area. The results can in future, with the aid of C-14 determinations, be correlated with the sequences obtained from the bottom deposits of lakes in the rift valleys and also with the known sequence of the northern hemisphere (van Zinderen Bakker 1958 and 1960).

The coastal lakes and lagoons where sea transgressions can be used to make world-wide correlations form another important starting point (Martin 1959). Inland deposits have to be calibrated with known geological or archaeological sequences or with C-14 chronology in order to be able to compare their pollen diagrams with those of other areas.

The results of East and Central African palynological research have not yet been published, but are promising for the watershed between the Nile and the Congo west of Lake Victoria, and also for the high Kenya mountains. At Kaisungor in western Kenya a mountain swamp is at present being investigated by the author. This swamp which is to-day situated in the upper reaches of the montane forest, started to form when the surroundings were practically treeless. This change in vegetation indicates a decrease in temperature. It is a common feature of the climate of East African mountains that the highest rainfall usually occurs in the montane forest belt, because of the maximum condensation of moisture in the upward moving air at that altitude. Below this belt the precipitation is usually much less, and above the montane forest the rainfall diminishes gradually, so that under special circumstances, as on Kilimanjaro, even desert conditions can occur. The details in rain distribution of course depend to a great extent on the exposure of the site under consideration and on the wind regimen.

A depression of the tree-line indicates a lower temperature and consequently drier conditions in the upper forest limits and in the Ericaceous belt. An upward shift of the forest, as was found in younger deposits at Kaisungor, therefore indicates a rise in temperature.

More evidence for a former lower temperature has been found during the preliminary investigations of the Kalambo deposits, near the southern end of Lake Tanganyika. The excavations, which have been carried out by Clark (1960 and personal communication), provide a wealth of archaeological material and also pollen-bearing deposits. The cooler conditions on this site lasted, according to C-14 age determinations, from at least 57,000 B.P. (before present) to 12,000 B.P. The lower temperature indicated by a number of plants coincided with locally wetter conditions. This fact could be explained by lessened evaporation and also by a downward shift of the vegetation belt, which brought the site temporarily near the belt of maximum rainfall.

Another proof for a decrease in temperature was found in N. E. Angola near Mufo. This material, which was also submitted by Clark, indicates a climate which was decidedly cooler than that of to-day. Mufo is situated at about the same latitude as Kalambo, but at an altitude of 750 m., whereas Kalambo lies at 1,260 m.

The cool periods at Kalambo, and probably also at Mufo, belong to the late Upper Pleistocene. Very interesting evidence on this same period has come to light in Tunisia and the Sahara. Deposits formed round artesian springs in Tunisia contained a pollen assemblage which is not fundamentally different from the present day pollen spectrum of the surrounding steppe. A number of grains however indicate a climate slightly cooler and a little more humid than that of to-day. This so-called "pluvial" is of Würmian age. The "interpluvials" were drier and hotter (Leroi-Gourhan 1958, van Campo 1958? and 1959).

Even on mountains in the central Sahara interesting proof has been found of a cooler and more humid climate during the late Upper Pleistocene. Pons and Quézel (1957) describe indications of a hygromesophyll forest with some *Alnus*, *Fraxinus* and *Tilia* for the Hoggar Mountains.

In postglacial times meso-xerophyll elements of the Mediterranean, semi-arid flora were widespread in the Sahara and North Africa (Hoggar, Tefedest, Mouydir, Tassili 'n Ajjer). Most of these plants disappeared when the desiccation set in about 3,000 years ago (van Zinderen Bakker 1958, Pons and Quézel 1957). The same workers analysed Procavia excrements from the Hoggar Mountains in the central Sahara. Although this material is not likely to provide a representative pollen spectrum, it nevertheless shows that 4,680 years ago a Mediterranean flora existed on these desert mountains (Pons and Quézel 1958). According to Hugot (personal communication), a similar pollen spectrum of Neolithic age from the Aïr has recently been dated at Saclay at 5,140 ± 400 B.P.

The pollen content of diatomites from the Tibesti Mountains in the eastern Sahara has also been studied. The pollen of these deposits, which are supposed to be less than 10,000 years old, indicates that a tropical flora lived in the valleys while the summits were covered with a forest of trees from temperate regions, such as *Cedrus* and *Pinus* (van Zinderen Bakker 1958).

Right at the other end of the continent Martin (1959) has studied a pollen sequence of the same age of Groenvlei, a coastal lake between George and Knysna, near Cape Town. Foraminifera and marine diatoms which were found in the lower horizons clearly show a marine transgression with a rise in sea level of ca. 3·3 m. This transgression must have occurred between 6,870 ± 160 and 1,905 ± 60 B.P. and could very well be contemporaneous with the Atlantic transgression in north-western Europe during the climatic optimum. The pollen indicates that until the return of freshwater conditions a heath vegetation with a climate similar to that of today existed. After that the coastal woodland became more important which indicates a higher rainfall. The climate of the coastal region of the Cape may not have changed considerably since the Middle Pleistocene, but it is important to know whether the temperature and humidity changes were contemporaneous with those of the interior of the continent.

The only pollen diagram which has been published from the interior of Southern Africa is that of Florisbad (van Zinderen Bakker 1957). This site, which became famous because the skull of *Homo helmei* and much palaeontological and archaeological material were found here, also provided pollen-bearing deposits of special interest. The oldest peaty layers, near the human skull, indicate a warm, semi-desert climate with a rainfall of about 125 to 250 mm. per annum. As the present-day rainfall in the Florisbad area varies between 450 and 500 mm. the lowest peaty horizon must have been formed during a nonpluvial which is, according to C-14 determinations, more than 43,960 years old. The pollen diagram shows in the younger part a change to a slightly wetter climate, above which it is interrupted and pollen is only found again in younger deposits between 28,460 ± 2200 and roughly 19,000 years ago. The climate as indicated by the pollen preserved in these late Upper Pleistocene layers began oscillating between wetter and drier conditions. The treeless vegetation gradually merged into a grassland, which could have been the warm-temperate grassland as is at present found on the plateau round Bloemfontein in the Orange Free State. It is however more likely that it was a mountain grassland of the cold alpine type as occurs at present in the Drakensberg above the tree-line. It is difficult to prove which type of grassland is presented in the pollen diagram. The change to alpine grassland would mean a considerable increase in humidity and a big drop in temperature.

Florisbad provides good evidence for an important change in climate during the Upper Pleistocene, causing the dry Karoo vegetation to give way to a much wetter temperate or alpine grassland. Many patches of Karoo vegetation which are at present found as far north and east as the line Lichtenburg-Heilbron-East London are indications of the slight equilibrium of this vegetation, which can easily turn either way. (Acocks 1953).

QUATERNARY CLIMATES

The Quaternary period was marked by extensive glaciations which are best known on the northern hemisphere. The sequence of four major glaciations has been substantiated, especially in Europe, by comprehensive geological, palaeontological, botanical and archaeological evidence. The chronology thus established has been supported by many dating techniques of which the modern C-14 method gives convincing proof of the exactness of the younger part of the time scale. In future the Potassium-Argon method will probably contribute substantially to the dating of the Middle and Lower Pleistocene. The temperature curves published by Gross (1958) and Woldstedt (1958) give representations of the three main sections of the last glacial, the Würm, and its many oscillations. Gross and Movius (1960) have published reviews about this period.

The last Quaternary glaciation is the most important for our present discussions and we may summarise its sequence as follows (Table I).

The preceding interglacial, the Eemian (Riss-Würm), was a period with a climate warmer than that of the postglacial and marked by a high ocean level. The first phase of the glacial, the cool humid Early Würm, ended about 47,000 years ago, when the Göttweig Interstadial began. This warmer period lasted for about 18,000 years and was followed by the Early Phase of the Middle Würm. The warmer Paudorf Oscillation, about 26,000 years ago, separated the Early Phase from the Main Phase of the Middle Würm. The Würmian glaciers had their maximum advance in this phase during the extremely cold and dry Brandenburg Stadial, which occurred about 18,000 to 20,000 years ago. Since then the climate has ameliorated gradually, but the Late Würm had again two major warmer oscillations, the Bölling and the Alleröd, at about 15,000 and 12,000 years ago, respectively. The last 10,000 years since the end of the glacial are mainly marked by the Hypsithermal Interval which coincided with a high ocean level between 9,000 and 2,600 years ago. (Flint 1957).

This climatic chronology, set up for Europe can, in general, be applied to other parts of the northern hemisphere. Evidence gradually coming from America shows remarkable similarity (Flint and Brandtner 1961). Very interesting in this respect are some of the results of the research done on the stratigraphy and pollen sequence of Pleistocene lake sediments in the Searles Basin by Flint and Gale (1958). The Wisconsin glaciation of Northern America was here found to be contemporaneous with a cooler, pluvial period, which began more than 23,000 years ago and lasted till about 10,000 years B.P. This youngest pluvial period of Searles Lake coincided also with the severe glacial of the Middle Würm and with the Late Würm in Europe. An earlier pluvial was roughly coeval with the Göttweig Interstadial in Europe. Fossil pollen and fossil aquatic molluscs indicate for these pluvials a decrease in temperature of probably 6 to 8° C.

Very important support for the hypothesis of a general decrease in temperature during the late Upper Pleistocene, even in the tropics, comes from Colombia (S. Am.) from the study of fossil pollen and geological data by Maarleveld and van der Hammen (1959) and van der Hammen and Gonzalez (1960). The pollen diagram of a core of 32 metres of chiefly lake sediments has been used for the construction of temperature, tree-line and precipitation curves. The Upper Pleistocene and Holocene section of the curves has been calibrated with radio-carbon dates.

The remarkable fact is that glacial and interglacial periods, which were contemporaneous with those in Europe, were found in the Andes at an altitude of 2,560 m. The temperature curve in general fits well with the curves published for the Würm by Woldstedt (1958) and

TABLE 1:
WÜRM-CHRONOLOGY AND RADIO-CARBON DATES
(acc. to Gross 1958)

			Radiocarbon Dates B.P.
Post Glacial			
Main Würm	Late Würm		10,000
		Alleröd Oscillation	12,000
		Bolling Oscillation	15,000
	Main Phase		*ca*. 17,000
	Paudorf Oscillation		25,000
	Early Phase of Main Würm		26,000
Göttweig Interstadial			29,000
Early Würm			*ca*. 47,000
Eemian = Riss-Würm Interglacial			

Gross (1958). Temperatures during the maxima of the Würm were 7°–8° C lower than today. During the warmest phases of the interglacials the temperatures were about 2°–3°C higher than at present.

The glacials in the South American tropics were periods with a higher precipitation. The late Würm was relatively dry. A lower temperature caused a downward shift of the tree-line, but a higher annual precipitation forced it upward. During the last maxima of the Würm the tree-line was about 800–1000 metres lower than to-day.

The pollen studies of Auer (1958) in Fuego-Patagonia also indicate a low temperature and a glaciation for the southern end of South America during the Würm.

Interesting evidence for Quaternary climates has also come forward from the studies of Emiliani (1955, 1958) on fluctuations of isotopic-temperature in deep-sea cores in the tropical Atlantic ocean. The results show that the temperature minima fit well with the maxima of the Riss and Würm glacials. The isotopic temperatures from sea-floor sediments suggest that the surface water of the Pleistocene tropical Atlantic ocean was approximately

6 8°C. colder than to-day. These results are of very great importance as they also point to a general decrease in temperature during the Ice Ages, even in the tropical oceans.

DISCUSSION

The foregoing records from other parts of the world have been enumerated in order to compare them with the data available from pollen sequences in Africa. Surveying the evidence provided by fossil pollen in Africa we see that scattered but consistent proof points to a lowering in temperature during the late Upper Pleistocene on the whole continent. This drop in temperature was generally not high. In East Africa a downward shift of the higher mountain vegetation belts of at least 500 to 600 m. can be visualised. This would imply a decrease in temperature of at least 3 C. Flöhn (in Woldstedt 1954) estimated the decrease in temperature in the tropics during the glacial period at 4°C.

I will try to give a general picture of the climatic changes which may have occurred under these circumstances in different areas in Africa.

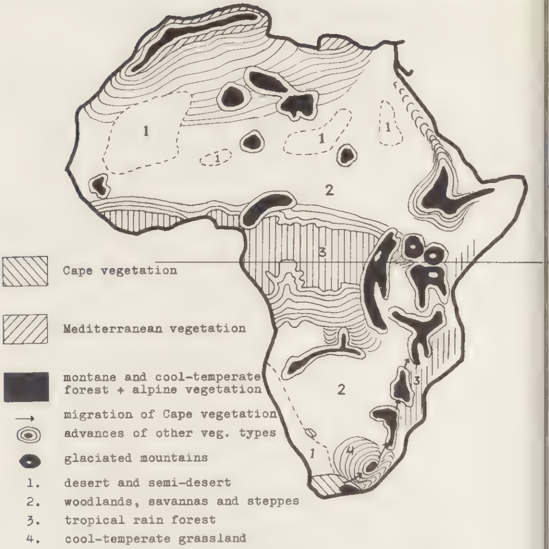
The Mediterranean area was probably directly affected by the cold climate of the European continent. The region at present receives its winter rain mainly from the depressions which travel from the Atlantic Ocean eastward. These cyclones must generally have passed much further south than to-day, because their northern tracks were closed by the ice-sheets and the glacial anticyclones, which occupied them (Zeuner 1959). Many more depressions must have travelled over the Mediterranean from west to east and brought a higher rainfall to this area. Their influence must even have reached far into the Sahara and have supported the distribution of mesohygrophyll forest on the desert mountains and sclerophyll macchia elements in the true Sahara.

The position in the S. W. Cape area is largely identical with that of the Mediterranean region. The southward movement of the high-pressure belt of about eight degrees in summer is at present partly responsible for the dry summer weather (Meteorological Service, R.N. and S.A.F. 1948). A northward movement of the high-pressure belt during a maximum of glaciation in Antarctica could have been responsible for a displacement of the tracks of the cyclones to lower latitudes, which would have brought more rain to the Cape area. It will be necessary to obtain pollen evidence and C-14 dates from the S. W. Cape area in order to establish how these cold and more humid periods fit in the Quaternary chronology.

The mountain areas in Africa must have been influenced differently by a lowering in temperature. A decrease in temperature should have had a direct influence on the condensation of moisture in the upward moving air, as already discussed. The maximum of condensation moved downwards and consequently lowered the montane forest belt. Lower regions, which formerly received less rain, had an increase in precipitation, because of this shift, while higher altitudes dried out more. Such a shift in the rainbelts had a much bigger influence than the slight decrease in temperature on the tree-line of montane forest, and the sclerophyll vegetation of the Ericaceous belt must have taken the place of the upper forest.

Higher up the mountains the decrease in temperature lowered the line of maximum snowfall and contributed to the growth of the glaciers on the highest mountains. It is therefore supposed that the cooler period was a period of extensive glaciation in Central Africa. The importance of a study of the position of the snow-line on the East African mountains for the explanation of the former climatic regimen is stressed by Flint (1959) in his survey of the available data. A temperature reduction on Mt. Kenya of 5°C and on Kilimanjaro of 7°C may probably be inferred.

This period of lower temperature during the Upper Pleistocene must have diminished the evaporation on the plateaux of East and Southern Africa, and have increased the soil humidity. More surface water was probably available for the vegetation and lakes probably enlarged their area considerably. This encouraged the distribution of rain forest and montane


1
1
1
1
2
3
3
2
1
4
Cape vegetation
Mediterranean vegetation
montane and cool-temperate forest + alpine vegetation
migration of Cape vegetation
advances of other veg. types
glaciated mountains
1. desert and semi-desert
2. woodlands, savannas and steppes
3. tropical rain forest
4. cool-temperate grassland

MAP IV. THE MOST IMPORTANT CHANGES IN VEGETATION DURING THE HYPOTHERMAL PHASE.

forest on the higher ranges and plateaux, and the spread of the woodland into the grassland in so far as the winter temperature did not prevent such migration. The area of the Karoo vegetation certainly diminished because of invasion of grassland. The extent of these movements cannot yet be established as much more data is required from various sites to support this explanation.

The main changes in the vegetation pattern of Africa during this period of lower temperature have been indicated on Map IV. No effort has been made to give a detailed representation as the number of sites which have been studied is still too small. In northern Africa the desert areas have been sketched in those parts which at present have the highest mean July temperature.

The lower temperature affected especially the elevated temperate areas of Africa because of the more widespread occurrence of frost. The mountain ranges, with their wide variety of habitats, must have been refugia for many frost-sensitive plants (Goodwin 1955). Most plant species therefore have been able to survive this climatic oscillation.

The higher humidity had its greatest influence in the arid and semi-arid regions where a small, but consistent, increase in soil humidity and rainfall caused a considerable shift in vegetation over wide areas. This is especially the case in the flat arid regions in the southern and northern part of the continent, where no topographical features limit a widespread migration of plants.

Most obvious is the advance of the Mediterranean vegetation into the desert. This migration has been substantiated by much evidence. The equatorial rain forest must also have gained much area, especially in Uganda and Katanga, where at present many relics still exist. It is very likely that the coastal area of Eastern Africa, with its present-day high temperature, was also covered partly by tropical rain forest. The mountain vegetation had descended to lower levels and may have penetrated into the drier vegetation types over wide areas. Many isolated forest clumps merged under these conditions. On the top of the highest mountains in East Africa the glaciation must have reached a maximum.

The grassland area of Basutoland pushed the semi-arid vegetation far to the south-west and covered the greater part of the Orange Free State and the southern part of the Transvaal. The temperate forests, of which small relics now exist along the south coast of the continent, extended their area to the north-east and merged into the montane forests further north. During this cooler period the Cape vegetation was able to migrate north on the eastern side of the continent along the mountain ranges of the escarpment.

The available botanical evidence here summarized points to a higher humidity in many parts of Africa during approximately the same period. Several chronologies set up for the Quaternary of Africa on geological, palaeontological and archaeological evidence make provision for a number of so-called pluvial periods. This theory can on botanical records be substantiated for one "pluvial" only. We do however not want to use this ambiguous term for this period as pollen data strongly suggest that a more appropriate name should be chosen. The term "pluvial" suggests conditions entirely different from those which prevailed and it would be better to give a name to this period in accordance with its main characteristic, the lower temperature. The name *hypothermal phase* would be much more appropriate and is proposed here for this phase, which was contemporaneous with the Main Phase of the Würm in Europe. We agree with much of the criticism of the pluvial theory, which has, in recent years, been coming from geological quarters (Cook 1957, Flint 1959? Pickering 1958 and Bishop and Posnansky 1960) especially as the theory has been formulated in East Africa on slender evidence, and has been applied with too much enthusiasm for the rest of the continent.

Evidence from periods older than the Upper Pleistocene, such as the distribution of relic vegetation, also points to a cooler and more humid climate than that of to-day, but this supposition cannot yet be supported by pollen analysis. Pollen data from the Post-Pleistocene in Africa are still too scattered to allow any general conclusions for the younger geological periods.

SUMMARY

The difficulties arising from using climatological maps for botanical purposes are discussed. A broad classification of climatic-ecological regions is proposed for the study of Quaternary plant distribution.

Discontinuous distribution and vegetation relics of a number of floras are described as indications of former different conditions. Special attention is paid to the Palaeotropical Flora, the Mediterranean, the Cape, and the Alpine Holarctic Flora, the Montane and Temperate Forests and the Karoo Flora.

The available evidence from fossil pollen is compared. The fossil pollen spectra of the late Upper Pleistocene strongly indicate a decrease in temperature of a few degrees centigrade for the whole of Africa. In most parts of the continent a higher humidity occurred during this cooler period. The influence of this climatic change is discussed for some areas. It is proposed to use the term "hypothermal phase" for this period and to avoid the term "pluvial", as not being appropriate.

The hypothesis of a world-wide lowering in temperature during the Main Phase of the Würm Glacial is supported. At present little fossil pollen evidence is available for younger and older periods in Africa.

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DISCUSSIONS

Dr. Brain: Does it seem reasonable to Dr. van Zinderen Bakker to associate glacial periods with reduced temperatures and inter-glacials with increased temperatures and so to extend these climatic changes back through the Pleistocene?

Dr. van Zinderen Bakker: Evidence is inadequate except for the Würm glaciation, but it seems probable that the changes were world wide and of cosmic origin and that similar conditions applied to earlier glaciations.

Prof. Balinsky: Would not lower temperature automatically result in more humid conditions without necessarily implying increased rainfall? The primary factor would thus be temperature, but the secondary factor which affects vegetation and animal life is precipitation.

Dr. van Zinderen Bakker: I would not disagree, but suggest that we emphasize temperature rather than rainfall.